

## LONG-DISTANCE DISPERSAL AND COLONIZATION IN THE BAY CHECKERSPOT BUTTERFLY, *EUPHYDRYAS EDITHA BAYENSIS*<sup>1</sup>

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**Abstract.** Dispersal, patch finding, and colonization abilities of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) were measured in field experiments. Butterflies released in non-habitat were capable of moving several kilometres to reach a distant habitat patch. However, their interhabitat movements appeared to be non-oriented, unless they were within 50 m of a suitable patch. To quantify colonization ability, I transplanted propagules of 100 postdiapause larvae each to 38 vacant habitats. Twenty-four transplants (63%) produced adults in the initial year, and 6 (25%) of these initially successful transplants persisted to produce adults one year later. Thus the chances of successful population establishment, given the presence of a gravid female on a vacant habitat, appear to be low (i.e., at most a 6.25% chance of persisting 2 yr). The present distribution of the butterfly suggests that hilly intervening terrain inhibits the colonization of distant habitat patches. These results shed additional light upon the dynamics of a metapopulation of the Bay checkerspot butterfly.

**Key words:** butterfly; colonization; dispersal; *Euphydryas editha*; metapopulation; orientation; patchy habitat.

### INTRODUCTION

The occasional movement of organisms between distant habitats is a phenomenon of great evolutionary and ecological importance. If the recipient habitats are unoccupied, dispersal creates the potential for colonization, an essential feature of the population dynamics of species prone to local extinction. Like gene flow between established populations, colonization may be crucially important in the population biology of species, and yet be so infrequent that it is almost impossible to quantify directly.

In this paper I examine the colonization process in the Bay checkerspot butterfly, *Euphydryas editha bayensis*. (By colonization I mean the colonization of new patches of habitat, not new types of habitat as in “weedy” organisms.) The Bay checkerspot presents something of a paradox, in that it has long been observed to be quite sedentary with respect to between-habitat movements (Ehrlich 1961, 1965, Gilbert and Singer 1973). Yet this butterfly is also prone to local extinctions, caused largely by climatic events such as the 1975–1977 California drought (Ehrlich et al. 1980, Murphy and Ehrlich 1980). The butterfly must somehow occasionally disperse to new habitats and found populations if its regional distribution is not to shrink inexorably in the face of local extinctions.

Resolution of this paradox may lie in examining the complete suite of characteristics related to colonizing success. The major features that should make an organism a good colonist are: (1) a propensity to leave

the natal habitat; (2) the ability to move long distances over intervening non-habitat; (3) the ability to locate new habitats; and (4) the capacity to establish populations from a small number of founders, once new habitats are reached. Few studies of colonization (e.g., Crowell 1973, Cole 1983, Schoener and Schoener 1983) have assessed all of these stages of the process. Previous work suggests that the Bay checkerspot butterfly is relatively reluctant to leave its natal habitat. However, its capacities for long-distance movement, patch finding, and establishment of new populations, are not known. This paper reports field experiments designed to test the capabilities of the Bay checkerspot butterfly to reach distant habitats and to found new populations. Experiments were conducted in March and April of 1987 and 1988.

### BACKGROUND AND STUDY SYSTEM

The Bay checkerspot butterfly is a univoltine host-specialist on annual plantain, *Plantago erecta*, and owl's clover, *Orthocarpus* spp., which grow in serpentine grasslands. The Bay checkerspot forms highly discrete local populations (Ehrlich 1961, 1965) on patches of serpentine grassland, which are scattered throughout the range of the butterfly on the San Francisco Bay Peninsula, California, USA.

Evidence for long-distance dispersal and colonization is apparent in the distribution of the Bay checkerspot in Santa Clara County, California. Near Morgan Hill, California, is a population of several hundred thousand adult Bay checkerspots, occupying an ≈2000-ha patch of serpentine grassland (Weiss et al. 1988). (This population and habitat patch are both referred

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to henceforth as MH.) Surveys in 1987 revealed that in the same region there existed nine small populations ranging in size from  $\approx 10$  to 400 adult Bay checkerspots, as well as numerous unoccupied patches of serpentine grassland supporting the larval host plant *Plantago erecta*. Harrison et al. (1988) examined 60 such patches, and found there to be 18 unoccupied patches as high in quality (an aggregate measure which included area, distribution of slope exposures, and abundance of host and nectar plants) as those patches which supported Bay checkerspot populations in 1987. The nine populations were all found on patches lying within 4.5 km of MH, while the unoccupied but suitable patches ranged from 4.6 to 20.8 km from MH (Fig. 1; Harrison et al. 1988). Hence distance from MH was a strong predictor of the occurrence of small populations in this region, indicating that dispersal from MH plays a major role in the butterfly's regional dynamics. MH and the populations around it may be considered a metapopulation, linked by extinction and recolonization.

The 1975–1977 drought eliminated all the then-known small populations of the Bay checkerspot butterfly within this region, although MH did not become extinct. Hence the nine small populations seen in 1987 were almost certainly founded at some time between 1978 and 1987. Two of the nine populations, in fact, are known not to have been present in 1986. This evidence suggests some recent colonization by the “sedentary” Bay checkerspot, over distances of up to 4.5 km.

## METHODS

### *Release of butterflies out of habitat*

Because the butterfly evidently tends to leave its habitat so infrequently it is impractical to measure spontaneous interhabitat movements. Therefore I studied vagility and patch-finding ability by experimentally moving butterflies out of their habitat. A target patch was chosen that was distant from MH (20.8 km to the south-southeast) and also  $> 10$  km from all other known Bay checkerspot habitats, save for a small patch (1.2 ha) some 0.3 km to its north. The 19.2-ha target patch included a 116-m hilltop. It was unoccupied by Bay checkerspots, but judged to be highly suitable for them, in 1987 (Harrison et al. 1988).

One thousand butterflies were captured at MH, marked and held overnight, and released the following morning. (Netting and enveloping 1000 butterflies during peak-flight hours required 14 person-hours; marking their wings with coded numbers from 1 to 10, using felt-tipped pens, required 12 person-hours.) One hundred butterflies were released in the center of the target patch, and 100 each from nine release points located 0, 0.05, 0.2, 0.5, 0.67, 1.0, 1.4, 3.0, and 5.6 km from a point on the northeast edge of the patch. The mark on each individual indicated its point of release. Each group had the same ratio of males to

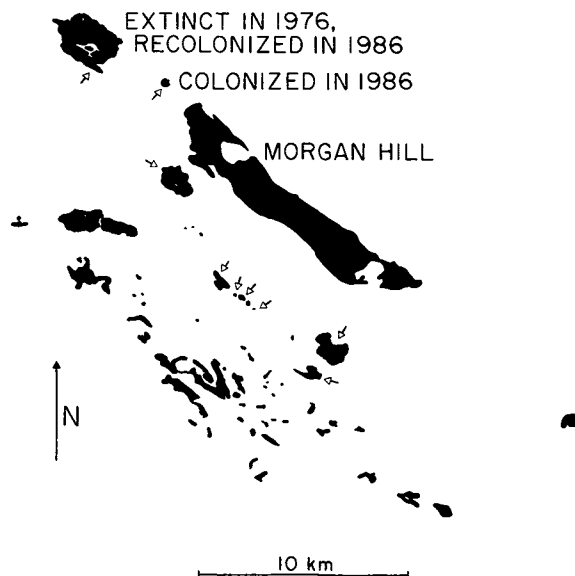


FIG. 1. The Morgan Hill metapopulation of the Bay checkerspot butterfly. Black patches are areas of serpentine grassland, supporting the host plants of the butterfly. The large patch labeled “Morgan Hill” supports the Bay checkerspot population MH, estimated at several hundred thousand adults in each year 1985–1988. Arrows indicate the nine patches which supported small populations of the butterfly (10–400 adults) in 1987 and 1988.

females, approximately 2.3:1, as was found in the sample from MH.

From each release point, the target patch was 225° to the southwest, approximately the same direction as that in which seven of the nine small populations lay with respect to MH. The intervening terrain was flat, and consisted of farm fields with scattered trees. US Interstate 101 passes between the target patch and the 3.0- and 5.6-km release points, just as it does between MH and seven of the nine small populations. To the human eye the target patch was clearly visible from every release point, since the hilltop was covered (as Bay checkerspot habitat generally is during the flight season) with brilliant yellow flowers of *Lasthenia chrysostoma* (Asteraceae).

For five consecutive days, beginning the day after the release, butterflies were recaptured on the target patch. The sex and point of release of recaptures were recorded, and their mass and wing lengths were measured. Rates of recapture as a function of distance from the point of release were calculated. These rates were compared with the predictions of various models of random movement, to assess whether the butterflies appeared to be orienting their flight non-randomly toward the target patch. The rate of recapture of the butterflies released in the center of the patch indicated the residence time and catchability of a butterfly given that it reached the patch, and so served to calibrate the predicted recapture frequencies. Differences between

the sexes in the rates of recapture of on- and off-site releases were also analyzed.

### Orientation

An additional 45–69 butterflies, in approximately 1:1 male-to-female ratios, were released at each of the three sites 0.2, 0.5, and 1 km from the target patch. Butterflies were placed on the ground until they flew away, and watched until they disappeared. The quadrant in which they were last seen—toward, away from, to the left, or to the right of the target patch—was recorded. The butterflies used were captured at MH earlier in the same day, and held in a cooler for no more than 6 h. Releases were performed under nearly windless conditions.

The proportion of released butterflies flying toward the patch was compared to the random expectation of 25%, to assess whether or not these first moves following release tended to be oriented toward the patch. (The 0.05-km release point was not used in this experiment, since the patch subtends 33% of the horizon from this distance.)

### Transplants

Bay checkerspot butterflies were transplanted to 38 unoccupied patches of serpentine grassland supporting *Plantago erecta* in order to evaluate the butterfly's ability to establish populations. Recipient sites varied from 0.1 to 120 ha in size, and included those deemed both suitable and unsuitable to support populations in the analysis of Harrison et al. (1988).

The propagule used in each transplant consisted of 100 late postdiapause larvae collected from MH. Postdiapause larvae were chosen for the following reasons. Adult females (the natural colonists) were considered unlikely to establish successfully under experimental conditions; it was feared that they would be excessively stressed by capture and transportation, and might simply flee upon release. Eggs and prediapause larvae lack mobility, hence a high degree of artifact could result from the experimenter's choice of the exact plants on which to place these life stages. Conversely, postdiapause larvae are capable of moving up to 10 meters per day (Weiss et al. 1987), and so have considerable capacity to move to preferred microhabitats. In addition, they are easily collected in large numbers and handled without injury.

A propagule size of 100 postdiapause larvae was chosen as an approximation of the number that could potentially survive from the egg output of a single founding female, under favorable circumstances. Maximum egg output is  $\approx 1000$  (C. Boggs, *personal communication*), but rates of larval survival are unknown. However, pupal survivorship has been measured at 50–75% (R. R. White, *personal communication*), so that under the assumption of a 1.6:1 ratio of males to females (Ehrlich et al. 1984), each female must produce at least 6–10 postdiapause larvae to replace herself.

This estimate must be adjusted upward to take into account mortality of late larvae and pre-reproductive adults. On average, it would probably take 2–15 females to produce 100 postdiapause larvae (M. C. Singer, *personal communication*).

At each recipient patch the intent was to provide each transplant with the maximum opportunity to succeed, given the characteristics of the site. Larvae were released into the best possible part of the habitat, using criteria established by previous work (e.g., Weiss et al. 1987, 1988). Larvae were placed in areas where *Plantago erecta* formed dense and extensive stands on a level or nearly level surface. When possible, level areas adjacent to both cool (north and east) and warm (south and west) slopes were used as release points. Larvae were collected on 19 and 20 February and transplanted on 21 and 22 February, 1987.

Recipient sites were monitored at least three times, at 3–7 d intervals or until butterflies were found, in both the 1987 and 1988 flight seasons. Each patch was visited during its approximate peak-flight period for the checkerspot, which depends on patch topography and which may be estimated by observing the phenological status of *P. erecta* and *Lasthenia chrysostoma*.

### Analysis of presence-absence data

In 1987 the patch distance from MH explained 76% of the variation in butterfly presence vs. absence on 60 patches in this system, under a simple model that assumed immigration rates to be negative exponential functions of distance (Fig. 2; Harrison et al. 1988). This model also indicated that “stepping-stone” migration between the small patches is unlikely to affect overall rates of colonization. Extrapolating the inferred rates of colonization into the future, the model predicted that, disregarding extinction, only seven more patches will become colonized in the next 40 yr.

However, the pattern of patch occupancy with distance shows an abrupt truncation at 4.5 km from MH (see Figs. 1 and 2) which cannot be explained by this model, nor by any other model that postulates immigration rates simply to be continuous functions of distance. Examining the reasons for this truncation may shed light on other factors besides distance which affect dispersal and colonization in this system. I consider several possibilities, through analyzing the residual variation in the presence-absence data shown in Fig. 2.

First, the nearer patches may block colonists before they reach more distant ones. Assuming there is no (or only a small) radius of attraction around a patch, such an effect ought to occur in proportion to the degree to which a patch's target size (*sensu* Pianka 1988) is reduced by interception from patches nearer MH. Target size, defined here as the width of a patch in the direction that faces MH, was measured from U.S. Geological Survey geologic maps of the serpentine patches. The shortest line between each patch and MH was drawn;

the target size is the distance between two lines parallel to this line and tangential to the patch. "Corrected target size" is the target size of a patch minus the portion that is intercepted by the target size(s) of patch(es) closer to MH.

Second, the seven populations to the southwest of MH are all separated from MH by flat and open terrain. This is not true of the two populations lying to the north of MH. But interestingly, the latter two were apparently founded in 1986, while the former seven must have been founded at least several years earlier, given their 1987 sizes of 10–400 adults. Conversely, nearly all of the unoccupied but suitable habitat patches are separated from MH by hilly terrain. Intervening topography may influence a patch's chance of receiving colonists from MH. Intervening topography was measured from USGS 15' maps by counting the number of 6.1-m topographic lines intersected by the shortest line from each patch to MH.

Third, even among presumably suitable patches, variation in their quality may influence colonizability. This would be especially true if dispersing females manifest "choosiness" upon arriving at a habitat patch. If so, patch area and other characteristics, such as host abundance, may explain some of the variation in patch occupancy. The aggregate index of habitat quality presented in Harrison et al. (1988) combines patch area, distribution of slope exposures, and densities of host plants *Plantago erecta* and *Orthocarpus* spp. and major nectar source *L. chrysostoma*.

Fourth, the direction in which a patch lies with respect to MH may influence its probability of becoming colonized. Prevailing winds or unknown aspects of the butterfly's orientation behavior may influence the directionality of flight. Unfortunately, of the 27 patches identified by Harrison et al. (1988) as being suitable checkerspot habitat, 22 lie between 210° and 240° southwest of MH (along the shortest connecting line). There is therefore insufficient variation in the data to test for directional biases.

For the 27 sites (9 occupied and 18 unoccupied), the deviation of the actual occupancy state (0 or 1) from the prediction of the distance-based model (Fig. 2; Harrison et al. 1988) was regressed on the following variables in separate single regressions: target size, corrected target size, intervening topography, area, and quality. This was repeated for a directionally homogeneous subset of patches, the 7 occupied and 15 unoccupied ones which lie to the southwest of MH.

## RESULTS

### *Out-of-habitat release experiment*

A total of 101 butterflies were recaptured, including twenty-nine (29%) of those released on the target patch. Fig. 3 shows the percentages that were recaptured from the out-of-habitat release points, as a function of distance from the release point to the target patch.

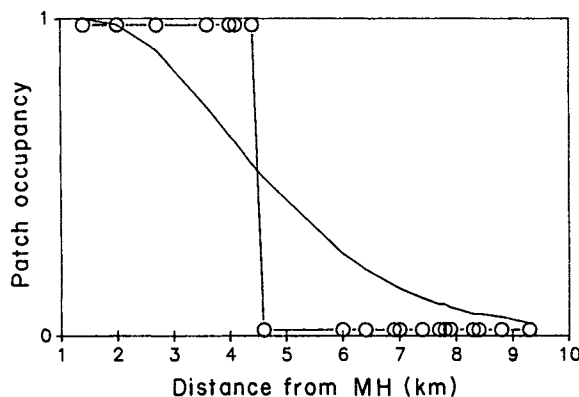


FIG. 2. Occupancy status of suitable habitat patches with respect to their distances from patch MH (Morgan Hill). Circles indicate patches; on the vertical axis, 1 = patches supporting Bay checkerspot populations, 0 = unoccupied patches. The curve indicates predicted occupancy status as a function of distance, based on a model which assumes 10 cumulative years of negative exponential colonization with no extinction. Data from Harrison et al. (1988).

Eighty percent of the 101 recaptures were made the 1st d after release. Recaptures per collector-hour declined sharply and monotonically from 4.4 on day 1, to 1.7 on day 2, to 0.9, 0.7, and 0.5 on days 3, 4, and 5. The median release point of the recaptured butterflies changed little in the first 3 d, varying between 0.05 and 0.2 km from the target patch (on days 4 and 5 only 2 and 1 butterflies were captured, respectively). It therefore appears that virtually all recaptured butterflies reached the patch within the 1st d. One male released at 5.6 km was recaptured on the patch <24 h after release. The second longest recorded move was by a female released at 3.0 km and recaptured on the target patch on day 4.

The 71% of the butterflies released on the target patch and never recaptured is high in comparison with daily rates of disappearance of marked checkerspots from the populations at Jasper Ridge (J. Baughman, *personal communication*). Perhaps many of these died or emigrated (actively or passively) in the 1st d following release. However, it is difficult to interpret the significance of this figure without knowing the catchability of the butterflies under the particular conditions of the experiment.

Winds from the north to northwest, up to 30–40 km/h, blew frequently during the experiment and during much of the 1988 flight season. These prevailing winds were at approximately right angles to the line from the release points to the patch. This suggests that neither passive movement to the patch, nor long-range olfaction, is likely to have been an important mechanism of patch location.

The rates of recapture with distance may be compared to a simple null model of random straight-line movement away from the release point with no distance-dependent mortality. In this model the expected percentage recapture from each release point equals

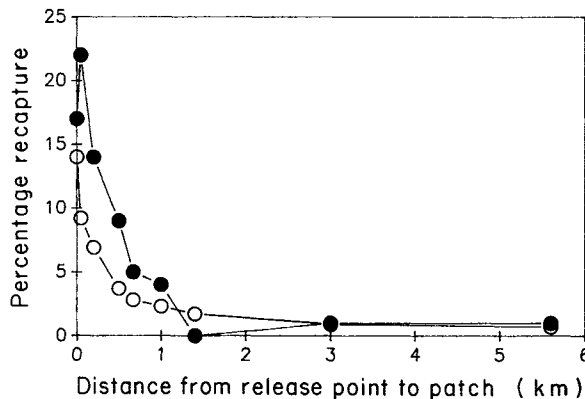


FIG. 3. Results of the out-of-habitat release experiment. ●: observed recapture frequencies on a target habitat patch of butterflies released at varying distances from it (0 = edge of target patch). ○: predicted recapture frequencies, calculated as (angle subtended by the target patch from the release point/360) × (% recapture of butterflies released within the target patch).

$$\frac{(\text{angle subtended by target patch}/360) \times (\% \text{ recapture from on-site release})}{(\text{MacArthur and Wilson 1967})}$$

The observed values are significantly higher than those predicted by this model ( $\chi^2 = 38.2$ , 8 df,  $P < .001$ ).

An alternative model for random movement is the negative exponential function (Wolfenbarger 1949, MacArthur and Wilson 1967), which likewise assumes straight-line movement but also includes distance-dependent mortality. This function declines more steeply with distance than the model described above. Therefore the observed recapture frequencies must be significantly higher than those predicted by a negative exponential random model.

Another alternative is a diffusion model. Using the techniques of Kareiva (1983), the observed recapture-with-distance curve (for first-day recaptures only, since so few butterflies were captured on days 2–5) was much more leptokurtic than would be expected under passive diffusion in a homogeneous environment (Kolmogorov-Smirnov  $D = 0.348$ ,  $n = 56$ ,  $P < .01$ ). However, a leptokurtic curve is to be expected when the target, in this case the habitat patch, is absorbing (Berg 1983). Thus, a diffusion model modified by the inclusion of an appropriate "settling" term might better fit the data.

Using the first model, the excess of observed over predicted returns is seen principally for the release points <1 km away. The only observed value which is higher than its expectation by more than its 95% confidence interval is the 0.05-km point. The data can be used to find the radius of detection of the patch by butterflies, if it is assumed that this radius effectively acts as a reduction in the distance between any point and the patch. Then the estimated radius of detection is the distance that, when subtracted from the distance between each release point and the patch, maximizes the

fit of the above model to the data. This distance is  $0.047 \pm 0.010$  km (jackknifed standard deviation). These data are therefore indicative of orientation ability over only very short distances, and of random movement over distances of several kilometres.

The ratio of males to females, 2.3:1 at release, increased in the overall recapture to 2.9:1. This is consistent with the higher catchability of Bay checkerspot males than females (Ehrlich et al. 1984). However, the ratio of recaptures of off-site to on-site releases did not differ significantly between males (57:18) and females (15:11) ( $\chi^2 = 1.24$ , 1 df,  $P > .10$ ), revealing no marked difference between the sexes in their abilities to reach the patch. In neither sex did mass or wing length differ significantly between on- and off-site recaptures.

#### Orientation experiment

No significant tendency was found for butterflies, released from the three points 0.2, 0.5, and 1.0 km from the patch, to fly initially into the toward-patch quadrant ( $\chi^2 = 0.81$ , 1.62, and 2.79 respectively, 1 df,  $P > .10$ ). Pooling over release sites, there was no significant tendency for either sex to fly toward the patch more frequently than the other (females 32%, males 36%;  $\chi^2 = 0.31$ , 1 df,  $P > .10$ ). The experiment was performed in the morning when winds were absent or light; when present, winds tended toward the left quadrant, but there was no significant tendency to fly in this direction (for 0.2, 0.5, and 1 km,  $\chi^2 = 1.40$ , 0.27, and 0.07, respectively; 1 df,  $P > .10$ ).

#### Transplant experiment

On 24 of the 38 transplant sites adult butterflies were found in 1987, the year in which the larval transplants were performed. Six of these 24 transplants persisted for a complete year and yielded adults in 1988. In both years the numbers of butterflies observed on each transplant site ranged from one to three; it would thus appear that populations did not grow rapidly in their 1st yr of establishment, between 1987 and 1988.

It is possible that some successful transplants could have been missed in the monitoring procedure. The probability of this is difficult to estimate. However, no butterflies were found in 1988 on transplant sites on which none were found in 1987.

Patch characteristics did not appear to determine the outcome of transplants in the first 2 yr. Patch area and quality correlated with neither first-year success (Mann-Whitney  $t_s = 1.24$  for area, 1.09 for quality; 24 and 14 df, respectively,  $P > .10$ ), nor second-year persistence contingent on first-year success (Mann-Whitney  $U = 71$  for area, 57 for quality; 18 and 6 df, respectively,  $P > .05$ ). This suggests that initially the transplant experiment measured primarily the stochastic demographic factors in population establishment (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972). These factors include variance in survivorship, fecundity, and sex ratio, and perhaps the frequency of mate

encounter. A behavioral tendency of checkerspot butterflies to emigrate at low densities (Gilbert and Singer 1973) may also play a role in establishment success or failure. Patch area and quality will presumably exert effects in the longer term, as extinctions of the transplanted populations occur.

The results of this experiment may be used to derive a very approximate estimate of the survival probabilities for newly founded populations. The 14 transplants which produced no adults initially are excluded from this calculation. The remaining 24 transplants began their first complete year with varying numbers of adults, including an average of perhaps (as previously explained) 2–15 females. Of these 24, 6 (25%) persisted through a complete year to produce second-generation adults. Twenty-five percent is thus a rough estimate of the yearly survival rate for very small populations. It is probably an overestimate of the first-year survival rate from single founding females. Thus,  $25\%^2$  or 6.25% is an estimate, most likely an excessive one, of the chance that a population survives for 2 yr following establishment. The Bay checkerspot would not appear to be a good colonizing species in the sense of having the capacity for rapid population expansion in vacant habitat. However there is undoubtedly a great deal of spatial and temporal variation in establishment success.

#### *Analysis of the pattern of distribution*

None of the factors studied (patch target-size, corrected target-size, area, quality, intervening topography) significantly explained residual variation from the simple distance model for butterfly presence/absence on the 27 patches. However, if the two patches to the north and the three patches to the southeast of MH are excluded, intervening topography emerges as a significant additional predictor of presence/absence on the 22 patches to the southwest of MH ( $r = -0.51$ , 20 df,  $P < .01$ ). A combination of topography and directionality may influence the dispersal of Bay checkerspots from MH to distant habitats. Since all of the suitable and unoccupied (in 1987) habitats were separated from MH by hilly terrain, this effect may explain the abrupt truncation of the distribution of butterfly populations at 4.5 km from MH.

#### DISCUSSION

Taken together, the results reported here present a picture of a rather poor disperser and colonist. In the release experiment, although individual Bay checkerspots were seen to have moved distances of 3 and 5.6 km to the target patch, movement to the patch from >50 m away appeared to be random. The orientation experiment reinforced the latter conclusion. These findings are similar to those for desert *Drosophila*, which move distances of several kilometres between oases but appear to be able to detect oases only from  $\leq 10$  m away (Yerington 1959, Coyne et al. 1987). If these

results are indicative, the butterflies that founded the nine small populations reached those patches by essentially random flight.

Furthermore, the chances of a gravid female checkerspot founding a population once she reaches a patch appear to be low. Under the conditions of this experiment, the probability of a newly founded population surviving one complete year is 25%, and that of surviving the first two years is 6.25% (or very likely less, for reasons explained in Results: Transplant experiment, above). As other studies have shown, establishment probabilities for colonists vary with propagule size (Crowell 1973), characteristics of the patch (Schoener and Schoener 1983), and other factors (e.g., presence or absence of competitors, Cole 1983). But the propagule size used here was above the average output of a single female, and many other considerations could be introduced which would further reduce the estimate of establishment probability. For example, dispersing females with full egg loads may be less capable of long-distance movement than those with fewer eggs. Much dispersal may occur late in the flight season, when chances of survival for progeny are reduced because the host plants have begun to senesce. The findings of random movement and poor establishment both imply that many more butterflies must leave MH than become successful colonists.

The pattern of patch occupancy suggests that a patch to the southwest of MH, surrounded by hilly terrain, is less likely to become colonized than one separated from MH by flat ground. Nearly all the remaining suitable but unoccupied patches in the study region lie to the southwest of MH and are separated from it by hills. The conclusion of Harrison et al. (1988) that seven more patches were likely to become colonized in 40 yr, based on the average rates that prevailed from 1978–1987, was therefore probably an overestimate.

Given the foregoing evidence, what is the most likely scenario to account for the colonization that has occurred in this metapopulation? One conclusion has already been alluded to. If establishment rates are low and movement is nearly random, and yet nine populations have indeed become established, it follows that the number of butterflies which leave MH must not be extremely small. Since population MH is so large, this does not necessarily conflict with the previous findings of low per capita rates of dispersal (Ehrlich 1961, 1965, Gilbert and Singer 1973). In other words, the key to the paradox of the Bay checkerspot's regional survival may not be adaptation for dispersal and colonization, but rather the existence within its range (until recently, when the others were destroyed by development) of a few large, persistent populations such as MH. Schoener and Spiller (1988) found similar dynamics in a Bahamian spider metapopulation: high turnover among numerous small populations, combined with high persistence because of the presence of some larger ones.

A second conclusion is more speculative. Temporal variation is probably a very important feature of colonization. Both the population size of MH and its per capita emigration rates undoubtedly vary strongly from year to year. Establishment success on the small patches must vary as well, driven by yearly rainfall and other climatic factors that affect the butterfly and its host plants. It is possible to envision that the founding of peripheral populations in the MH metapopulation occurs only during occasional boom years, when high emigration from MH combines with favorable establishment conditions, and perhaps with particular wind patterns. To the extent that colonization is episodic, it will be difficult to interpret and predict the dynamics of this metapopulation based on its present pattern.

In conclusion, the major elements of colonization in this butterfly metapopulation appear to be the following: high total (not per capita) rates of leaving from the source population, MH; random movement until a small radius of detection around a patch is reached; low chances of establishment; less ability of dispersers to cross hilly than flat terrain; and some influence, at present poorly understood, of compass direction. Though colonization is important to the Bay checkerspot's regional distribution and to its persistence in the long term, there is little evidence to suggest that it is a "colonizing species" in the classic sense.

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#### LITERATURE CITED

- Berg, H. 1983. Random walks in biology. Princeton University Press, Princeton, New Jersey, USA.
- Cole, B. J. 1983. Assembly of mangrove ant communities: colonization abilities. *Journal of Animal Ecology* 52:349–355.
- Coyne, J. A., S. H. Bryant, and M. Turelli. 1987. Long-distance migration of *Drosophila*. 2. Presence in desolate sites and dispersal near a desert oasis. *American Naturalist* 129:847–861.
- Crowell, K. L. 1973. Experimental zoogeography: introductions of mice to small islands. *American Naturalist* 107:535–558.
- Ehrlich, P. R. 1961. Intrinsic barriers to dispersal in the checkerspot butterfly. *Science* 134:108–109.
- . 1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. *Evolution* 19:327–336.
- Ehrlich, P. R., A. E. Launer, and D. D. Murphy. 1984. Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. *American Naturalist* 124:527–539.
- Ehrlich, P. R., D. D. Murphy, M. C. Singer, C. B. Sherwood, R. R. White, and I. L. Brown. 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia* 46:101–105.
- Gilbert, L. E., and M. C. Singer. 1973. Dispersal and gene flow in a butterfly species. *American Naturalist* 107:58–73.
- Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist* 132:360–382.
- Kareiva, P. M. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* 57:322–327.
- MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Murphy, D. D., and P. R. Ehrlich. 1980. Two checkerspot subspecies: one new, one on the verge of extinction. *Journal of the Lepidopterists' Society* 34:316–320.
- Pianka, E. R. 1988. *Evolutionary Ecology*. Harper and Row, New York, New York, USA.
- Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. *Theoretical Population Biology* 3:406–433.
- Schoener, T. W., and A. Schoener. 1983. The time to extinction of a colonizing propagule of lizards increases with island area. *Nature* 302:332–334.
- Schoener, T. W., and D. A. Spiller. 1987. High population persistence in a system with high turnover. *Nature (London)* 330:474–477.
- Weiss, S. J., D. D. Murphy, and R. R. White. 1988. Sun, slope and butterflies: topographic determinants of habitat quality in *Euphydryas editha*. *Ecology* 69:1486–1496.
- Weiss, S. J., R. R. White, D. D. Murphy, and P. R. Ehrlich. 1987. Growth and dispersal of larvae of the checkerspot butterfly *Euphydryas editha*. *Oikos* 50:161–166.
- Wolfenbarger, D. O. 1949. Dispersion of small organisms. *American Midland Naturalist* 35:1–152.
- Yerington, A. P. 1959. The atomic age and the vinegar fly. *Proceedings of the 51st Annual Meeting, Dried Fruit Association of California, April 1959, Fresno, California, USA*.

#### NOTE ADDED IN PROOF

The sites of the 24 initially successful transplants were monitored again during the 1989 flight season. Of the six transplants which were found to be extant in 1988, four remained. Surprisingly, butterflies were also found on five of the sites on which they were not found in 1988. Fresh individuals were found, making 1989 immigration an unlikely explanation. Several other possibilities exist: (1) The five sites may have become newly colonized in 1988. (2) I may have missed the butterflies on these sites in the 1988 monitoring. (3) The

butterflies seen on the five sites in 1989 may have come from larvae (the progeny of 1987 adults) which underwent a 2-yr diapause in response to drought.

The study region experienced a moderately severe drought in 1987–1988, receiving less than half of the average seasonal (November–April) rainfall. *Plantago* and *Orthocarpus* senesced several weeks before average. This, seemingly, would make 1988 a difficult year for dispersers to get established.

That butterflies were missed in the monitoring seems quite

possible for two of the sites, which were the two largest transplant sites (121 and 79 ha). However, the other three were <1 ha in area, and relatively easily searched.

Facultative multiple-year diapause occurs in numerous Lepidoptera, perhaps as an adaptation to environmental unpredictability (Powell 1986). It has never been shown to exist in *E. editha bayensis*, but several observations suggest it may: (a) In Sierran populations of *E. editha*, unusually large diapausing larvae have been found, during the adult flight season, beneath defoliated patches of their host plant (M. C. Singer, *personal communication*). (b) *E. e. bayensis* reared in the laboratory frequently re-enter diapause when they are fed wilted plant material (M. C. Singer and R. R. White, *personal communication*). (c) A very small proportion of diapausing larvae

found in the field are in instars beyond the fourth (R. R. White, *personal communication*). This is a question which invites further experimental study, since (if true) it could play an important role in the persistence of populations through adverse years.

These three possible explanations are, of course, not mutually exclusive. But in any case, it would appear that *E. editha bayensis*' establishment abilities are higher than was suggested by the original interpretation of the transplant results.

#### *Literature Cited*

Powell, J. A. 1986. Records of prolonged diapause in Lepidoptera. *Journal of Research on the Lepidoptera* 25:83-109.